



A new scalpellid (Cirripedia); a Mesozoic relic living near an abyssal hydrothermal spring*

William A. Newman

Abstract. A large stalked barnacle, *Neolepas zevinae* gen. et sp. nov., has been discovered living attached to ferriferous crust of a hydrothermal spring at 2600 metres on the crest of the East Pacific Rise. Comparisons with fossil and extant genera place the new genus as intermediate between the levels of organization found in *Eolepas* (Upper Triassic) and *Calantica* (Upper Jurassic-Holocene). Comparison with the ontogenetic stages of the advanced genus *Pollicipes* (? Upper Jurassic/lower Eocene-Holocene) indicates that *Neolepas* is represented by an 8-plated ontogenetic stage between the 6- and 13-plated stages of development. From these morphological and ontogenetic comparisons it is inferred that *Neolepas* represents the most primitive living scalpellid, a relic of Mesozoic age.

Habitat also favors the interpretation that *Neolepas* is a relic form, having found refuge near deep hydrothermal springs. Such a refuge may have been attained in the late Mesozoic when predation pressures on sessile organisms are inferred to have dramatically increased. Though immigration into the hydrothermal environment by deep-sea stocks is a distinct possibility, in the present case, the route appears more likely to have been from relatively shallow waters of warm and tropical seas where tectonically active rifts intersect continental crust, and perhaps where islands are forming along ridge crests.

INTRODUCTION

Unusual environments are often inhabited by novel organisms and submarine hydrothermal springs have proved no exception in this regard (*see* Corliss et al., 1979). Since the first photographs of animals from certain hydrothermal springs of the Galapagos Rift Zone became available several years ago, it was obvious that if barnacles were to be found there, they would likely be of some unusual type. Barnacles have exploited virtually all other marine environments, so it seemed likely that they would occur there. It was therefore especially exciting when a half dozen specimens of a most singular barnacle were recently recovered from a hydrothermal spring off central Mexico.

The specimens represent a new genus and species, *Neolepas zevinae*. *Neolepas* has important implications in interpretations of the evolution of the Scalpellidae. The Scalpellidae, the largest family of the Lepadomorpha, has recently been revised (Zevina 1978a, b). After the systematic position of *Neolepas* is established, it becomes possible to discuss the geologic time and evolutionary circumstances under which it or its immediate ancestors likely became adapted to the hydrothermal environment.

HABITAT AND BIOTA

The present material was taken from the crest of the East Pacific Rise off the west coast of Mexico. The general topography of the region has been documented by Normark (1976). Francheteau et al. (1979) provide an artist's view of the porous sulfide edifices constructed by hydrothermal activity there. The sulfides were of predominantly zinc, copper and iron. Hydrothermal environments of submarine continental crust must

* Contribution of the Scripps Institution of Oceanography, new series.

vary widely in their chemistry (P. Lonsdale, *personal communication*). Oceanic hydrothermal environments, conversely, although varying somewhat from spring to spring along a rift and from rift to rift, are likely quite similar in their characteristics. However, the very low concentrations of manganese at 21°N, as compared to the Galapagos situation, is notable (Francheteau et al., 1979) and this will be taken up below concerning metals of the hydrothermal environment and the barnacle. Corliss et al. (1979) summarize the situation surrounding the Galapagos Rift zone, a few thousand kilometres south of the *Neolepas* site:

"Analyses of water samples from hydrothermal vents reveal that hydrothermal activity provides significant or dominant sources and sinks for several components of sea water; studies of conductive and convective heat transfer suggest that two-thirds of the heat lost from new oceanic lithosphere at the Galapagos Rift in the first million years may be vented from thermal springs, predominantly along the axial ridge within the rift valley. The vent areas are populated by animal communities. They appear to utilize chemosynthesis by sulfur-oxidizing bacteria to derive their entire energy supply from reactions between the seawater and the rocks at high temperatures, rather than photosynthesis."

According to Corliss et al. (1979), the animals collected in the Galapagos Rift hydrothermal springs proved remarkable: clams resembling the unusual family Vesicomidae, mussels belonging to a new genus of Mytilidae, limpets of a new family, and pogonophorans of a new genus of Vestimentifera. A fish and crab peculiar to the area have also been observed. Some of these animals, such as the vestimentiferan, apparently have their closest relatives in deep water whereas others such as the true crabs hold their closest affinities with shallow water forms. Radiometric dating of shells from around an apparently expired vent suggested they were not more than 10 to 20 years old, indicating the minimum age of thermal activity at the spring was of the same order. Population structure differed from vent to vent, but individuals within a population were much the same size suggesting single colonizations in various vent areas (Corliss et al., 1979).

Vents are ephemeral and the exact locations of new ones unpredictable in space and time. But active rift zones persist for millions of years, and hydrothermal springs must have existed since the earth cooled sufficiently to allow the oceans to form; that is, before the origin of life. Therefore, other things being equal, species with adequate means of dispersal could persist indefinitely. But hydrothermal activity along rifts must at times shift more rapidly than can be compensated for by dispersal, and extensive extinctions have likely occurred. Furthermore, new forms must occasionally become adapted to the hydrothermal environment and such immigrations would, on occasion, cause extinctions through competition or predation.

It is important to attempt to determine the geological time an animal or its ancestor first became adapted to the hydrothermal environment. It is already apparent that the hydrothermal animals themselves are highly endemic, and therefore the geologic age at the generic level should be correspondingly great (Ekman, 1953). It will be instructive to know the degree of endemic similarity between vent regions; if it is high, dispersal between vent regions is low and vice versa.

The barnacle described here is endemic at the generic level. But it is the first cirriped from a hydrothermal spring, so the problem of regional endemism cannot be addressed. On the other hand, the scalpellid barnacles have a fairly good fossil record (*see* Newman et al., 1969). Therefore, upon determining its systematic position, its probable geologic age can be inferred.

DESCRIPTION

Family SCALPELLIDAE Pilsbry, 1907:3

Subfamily LITHOTRYINAE Gruvel, 1905:8 & 96

(*nom. correct.* Zevina, 1978a: 1000, *pro* Lithotrynae Gruvel, 1905)

Diagnosis.—Scalpellids with 8 capitular plates (rostrum, carina, terga, scuta and one pair of latera); peduncle with numerous whorls of calcareous scales. Hitherto represented only by the genus *Lithotrya*.



FIGURE 1. *Neolepas zevinae* gen. et sp. nov.: The first paratype (British Museum; Nat. Hist.) reg. no. 1979·209, $\times 2.5$.

Neolepas gen. nov.

Diagnosis.—A lithotryine with fully developed capitular plates and strong, imbricating peduncular scales in whorls of more than 8, which, once developed, are retained throughout life. Type of the genus: *N. zevinae* sp. nov.

Neolepas zevinae sp. nov.

Diagnosis.—As for the genus.

Material.—Attached to ferriferous crust from near hydrothermal springs on the crest of the East Pacific Rise (20°50'N; 109°W) at a depth of 2600 m. ALV 915, rock-4, 21 April 1979. Temperature field estimated to be from near ambient (1.5°C) to 5°C (R. Ballard, *personal communication*).

Deposition of types.—Holotype, USNM Cat. No. 172581; first paratype, British Museum (Natural History) Reg. No. 1979·209; ontogenetic stages, USNM Cat. No. 172582.

Description.—A hermaphrodite resembling *Pollicipes mitella* (Linné) in form, but having a capitulum formed of but 8 plates homologous to those of *Lithotrya* (Fig. 1). The animal is intrinsically white, with the surface of the plates marked only by faint growth lines beneath a transparent cuticle.

The capitular plates, and especially the older peduncular scales which increase in age towards the point of attachment, are stained brownish red by a thin, ferromanganese deposit. The surface of the capitulum of the 2 largest specimens was covered with randomly spaced folliculinid cases which, preserved in 80% ethanol, were blue green.

The imbricating, triangular, projecting, spine-like peduncular scales form as min-

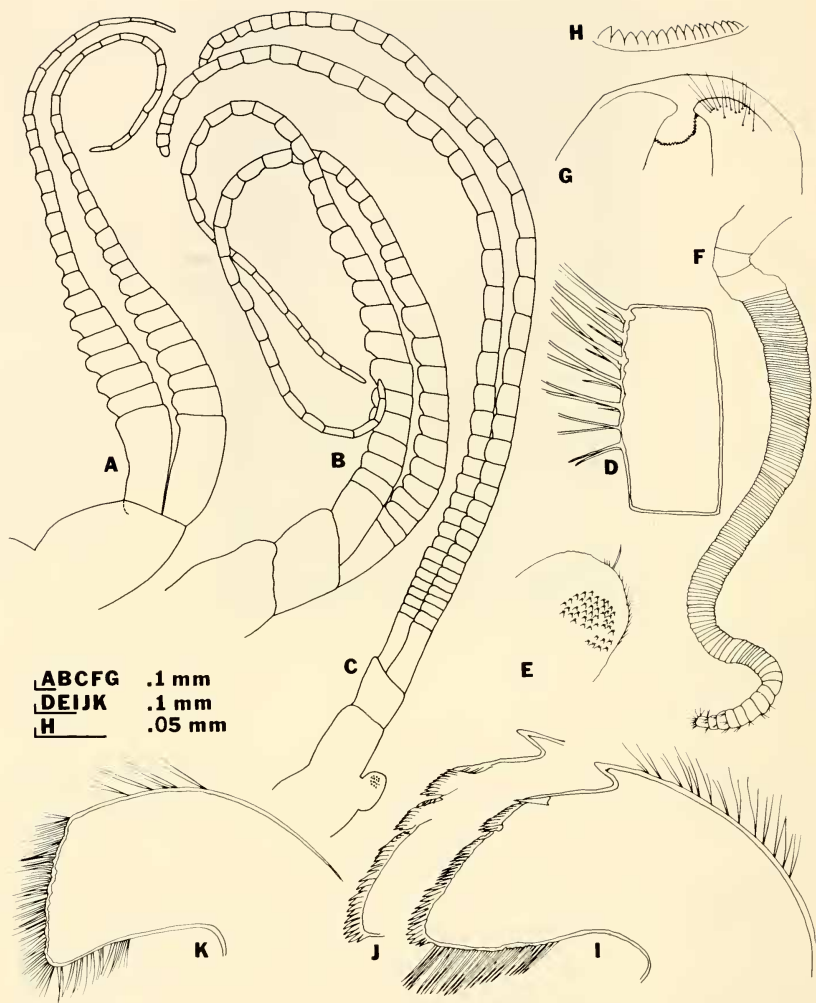


FIGURE 2. *Neolepas zeviniae* gen. et sp. nov.: Arthropodal structures of first paratype: A, cirrus I; B, cirrus II; C, cirrus VI and caudal appendage; D, intermediate article of cirrus VI; E, caudal appendage enlarged; F, penis; G, labrum; H, crest of labrum; I, left mandible; J, cutting edge of right mandible; K, first maxilla.

isculc points in the growth zone immediately below the capitulum. These points grow longer and broader and become more projecting, as successive whorls are added. This process is the same as that described for scalpellids in general and is markedly different from the specialized situation in *Lithotrya*, where the scales are periodically shed (Darwin, 1851). In *Neolepas*, whorls so formed are somewhat irregular and difficult to follow around the circumference of the peduncle, but they appear to be composed of about 12 scales each in the paratype.

The 6 specimens ranged from approximately 3.5 to 58 mm in total length. In the

A-C 1 mm

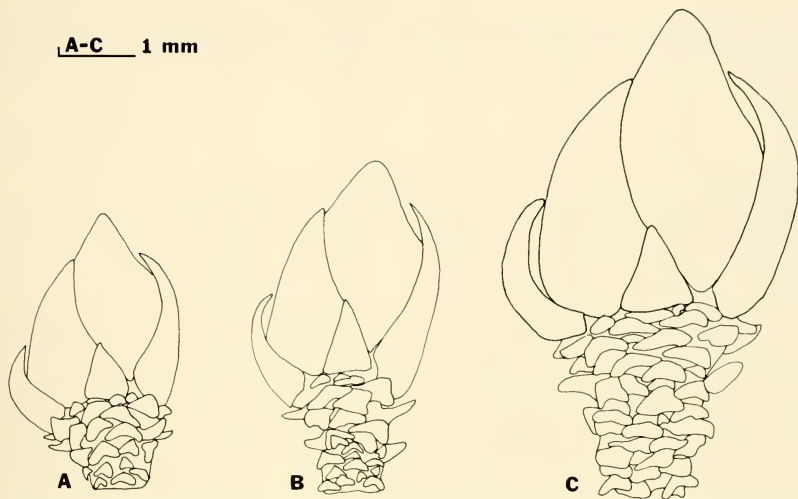


FIGURE 3. *Neolepas zevinae* gen. et sp. nov.: Juvenile stages in which the height of the capitulum exceeds the height of the peduncle (cf. Fig. 1).

3 smallest specimens the peduncle is less than half the height of the capitulum (Fig. 3). But this proportion reverses itself with further growth and in the paratype (Fig. 1) the peduncle is nearly twice, and in the holotype more than twice (41 to 17 mm), the height of the capitulum. This allometry accounts for the obvious addition of new peduncular scales compared to the less obvious growth increments in the capitular plates in the larger specimens. The result is that the capitulum comes to stand proportionately higher above the substratum with increasing age and, since the ovaries occupy the peduncle, there is more space for them. Placing the capitulum well above the substratum may be advantageous in insuring that the vital organs are well above the reach of some predators and that the trophic apparatus is in water of relatively undisturbed laminar flow.

The penis is well developed, the female genital apertures were observed at the bases of the first cirri and the holotype was brooding eggs. This indicates that the individuals are hermaphroditic. However, no complementary males were found between the occludent margins of the scuta, in the inner concave surface of the rostrum or, upon dissection, in the mantle cavity, and there are no pockets on the interior of the scuta. Thus the species appears to be purely hermaphroditic.

Trophi and cirri are designed for capture and manipulation of fine particles to an extraordinary degree (Fig. 2). The fragile nature of the cirri indicates that net casting must be extremely slow and then only into gentle currents.

The crest of the labrum, flanked by a pair of relatively small mandibular palps, bears a single row of minute, sharp teeth. The unique mandible is also provided with very fine denticles on the second and third tooth and along the very broad inferior angle. The combs formed by these fine teeth curve around onto the anterior surface of each mandible where they are in a position to scrape the crest and posterior (inner) surface of the labrum, as well as direct food pushed to them from behind by the maxillae, toward the mouth. Both the first and second pairs of maxillae are undistinguished, other than being simple and clad with very fine setae.

The cirri are uncommonly long, beginning with the first and second pairs in which the distal portions of the rami are antenniform. The third cirri resemble the remaining pairs. The unarticulate caudal appendages are small. Cirral counts are:

		First paratype						
		I	II	III	IV	V	VI	c.a.
R	a	25	33	45	47	34	37	1
	p	30	34	40	39	34	40	
L	a	24	33	44	49	46	47	1
	p	30	35	?32	36	39	39	
		Holotype						
R	a	31	35	47	54	58	60	1
	p	24	38	48	54	66	63	
L	a	30	36	47	56	?55	?54	1
	p	28	34	50	58	?59	?60	

Incubating eggs were found in the largest individual, as a single layer, in a pair of ovigerous lamellae of approximately 12 mm diameter. Each lamella was attached by a "Y"-shaped ovigerous frena on either side of the mantle cavity, and contained approximately 220 ellipsoidal eggs each measuring about 300 by 500 μm . Unfortunately, the eggs were at an early stage of development, and it could not be determined whether the larvae were to be released as nauplii or cyprids. If nauplii, it likely would have been possible to determine whether or not they would have been planktotrophic. Since this information is important in considerations of dispersal, it is regrettable that it was unavailable. But egg size in *Neolepas* is unusually large and this will be briefly considered in the discussion.

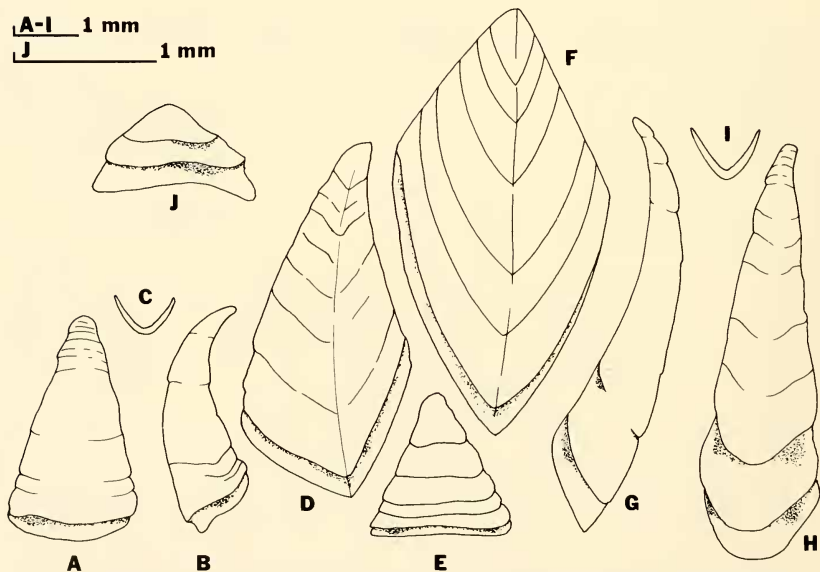


FIGURE 4. *Neolepas zeviniae* gen. et sp. nov.: Disarticulated capitular valves and a peduncular scale of a paratype (lateral views are of right side): A-C, frontal, lateral and cross-sectional views of rostrum; D-F, lateral view of scutum, median latus and tergum respectively; G-I, lateral, dorsal and cross-sectional views of carina; J, lateral view of a peduncular scale.

The genus has been named *Neolepas*: Neo—Greek *neos* (recent) + *lepas*—Greek *lepas* (shellfish); a Recent (Holocene) form inferred to have stemmed from an ancient

(*Eolepas/Archaeolepas*) lepadomorph lineage. The species has been named for Dr. Galina B. Zevina, in appreciation of her numerous contributions to our knowledge of the thoracican cirripeds, and especially for her recent revision of the living Scalpellidae (1978*a, b*).

DISCUSSION

Affinities

If one takes the structural data at face value, *Neolepas* must be assigned to the previously monotypic subfamily Lithotryinae. *Lithotrya* then is its closest relative and several species are found inhabiting primarily intertidal limestone in the western Atlantic and Indo-West Pacific. *Lithotrya* encompasses the only burrowing thoracican cirripeds, but this habitat alone is hardly grounds for erecting a new genus for the new form from the hydrothermal spring; there are a number of important structural differences.

Lithotrya is specialized for burrowing, as deduced by Darwin (1851). These specializations include (1) reduction of the rostrum and to some extent the single pair of latera, sometimes to mere rudiments, since the rostrum is no longer needed to protect the basal portion of the occludent scutal margin and the latera have become involved in forming, with the carina and terga, a plug in the burrow when the animal is withdrawn; (2) dimorphism in the peduncular scales, those surrounding the base of the capitulum being larger than those clothing the bulk of the peduncle; (3) small size and low profile of peduncular scales, forming a many-faceted calcitic grinding surface to attach primarily aragonitic limestone (chemical dissolution in burrowing may also be involved); (4) secretion of a calcareous cup or pad of cement attaching the animal near the base of the burrow; and (5) periodic molting and replacement of the peduncular cuticle and scales that totally replaces the grinding surface, a process unique to *Lithotrya*.

These characters readily separate *Lithotrya* from *Neolepas* at the generic level, but they do not preclude the two genera being in the same subfamily. The distinguishing features of *Lithotrya* are specializations to burrowing that are readily derivable from a *Neolepas*-like ancestor.

Position of the Lithotryinae

Broch (1922), without an appropriate explanation, placed *Lithotrya* as a derivative of the higher pollicipoid, *Protomitella*. This would require its being a reduced form having lost at least the subcarina and supplementary whorl of capitular plates. Broch, following Pilsbry (1908), was very much concerned with the structure and distribution of males among the scalpellids and came to the conclusion that they were absent in all higher forms. Males are absent in *Lithotrya* and this automatically made it a higher form. But the value of males in ranking genera is dubious since in the genus *Ibla* alone there is a pure hermaphrodite, a hermaphrodite with complementary males and a species in which the female is accompanied by dwarf males. Furthermore, it has been discovered that complementary males are even found in certain relatively advanced balanomorph barnacles (McLaughlin and Henry, 1972).

Zevina (1978*a*) places the Lithotryinae as the first subfamily of the Scalpellidae in her important revision of the extant members of this family. She arranges the remaining genera essentially in ascending phylogenetic order of increasing complexity according to the criteria set forth by Drushchits and Zevina (1969). Foster (1978) independently came to the same conclusion and places *Lithotrya* at the stem of scalpellid evolution as far as living genera are concerned. However, in the second part of her revision of the scalpellids (Zevina, 1978*b*), apparently for the same reasons as Broch (1922), she places the Calanticinae rather than the Lithotryinae at the stem of her phylogenetic tree.

Broch (1922) took the fossil record into account in drawing phylogenetic conclusions, and he championed the fundamental nature of the 5 ontogenetically chitinous,

primordial valves in cirriped evolution. However, the rather simple forms, *Cyprilepas* (Wills, 1963) with its bivalved chitinous carapace, *Praeilepas* (Chernyshev, 1930) with its 5 chitinous valves and *Eolepas* (Withers, 1928) with its rostrum, had yet to be discovered. And, at the time, it was not realized that the Paleozoic Machareidia, with their numerous whorls of calcareous imbricating plates, were not barnacles (Withers, 1928). Furthermore, neither Broch (1922) nor Zevina (1978*a, b*) drew upon the ontogenetic data in *Pollicipes* that Broch (1922) had so carefully described and Drushchits and Zevina (1969) had recognized as important, in drawing phylogenetic inferences. Finally, neither Broch nor Zevina had *Neolepas* to ponder. What bearing then does fossil and ontogenetic evidence have in determining the position of the Lithotryinae in the evolution of the Scalpellidae?

Fossil and Ontogenetic Evidence

Pollicipes is considered the most advanced of the generalized members of the pollicipoid Scalpellidae (Broch, 1922; Zevina, 1978*b*), and the postlarval ontogenetic stages in extant *Pollicipes polymerus* Sowerby are described by Broch (1922). It is remarkable to observe that there is virtually a one-for-one correspondence between the appearance of fossil cirripeds through time and this ontogenetic sequence. Only the "Neolepas or 8-plated stage," recapitulated in the ontogeny of *Pollicipes*, is missing from the fossil record. By placing *Neolepas* in the open position (Fig. 5), we should be able to infer the geologic age of the *Neolepas* grade of evolution with considerable confidence, even though it is only known from the Holocene.

Figure 5 has been prepared to aid in the comparison between the extant and fossil genera involved here, and in visualizing their alignment with the ontogenetic stages in *Pollicipes*. The oldest fossil evidence for the Cirripedia is found in the Silurian lepadomorph *Cyprilepas* (Wills, 1963). However, the lepadomorphs descended from free-living ancestors at an ascothoracican level of organization (Newman et al., 1969; Newman, 1974). Unfortunately ascothoracicans are known only as far back as the Cretaceous, and then by fossil traces made by the more specialized wholly parasitic type, like *Ulophysema* (Madsen and Wolff, 1965). But one cannot distinguish the bivalved carapace of generalized ascothoracicans from some forms referred to the archaeocopid ostracods (Lower Cambrian–Lower Ordovician; Sylvester-Bradley, 1961). Therefore, because the ascothoracican level of organization cannot have been less than Silurian, and because fossils that could represent them have been found in the Cambrian, the latter age is inferred here. The important point for present purposes is, however, that the ancestral free-living form, represented for the most part by the generalized characteristics of an extant ascothoracican such as *Synagoga*, is passed through in the ontogeny of all cirripeds as the cyprid stage, as illustrated in Fig. 5.

The cyprid larva, when first attached to the substratum, can be considered representative of the "Cyprilepas stage" in the evolution of barnacles as well as in the ontogeny of *Pollicipes*, because it is the closest living approximation of that level of organization in all cirripeds above the Ascothoracica. Indeed, if an attached cyprid capable of feeding and reproduction were found, and there were no contrary evidence, it should be assigned to the Silurian family Cyprilepadidae.

The next, or what can be referred to as the "Praeilepas stage" in the ontogeny of *Pollicipes*, has the formerly bivalved carapace divided up into 5 plates; the paired terga and scuta of each side and the carina protecting the dorsal articulation. At this stage, all 5 plates are of a prismatic chitinous construction; the so-called primordial valves of Darwin (1851:22). The bivalved carapace of *Cyprilepas* is prismatic chitin (Wills, 1963), and this is the condition in the 5-plated stage in the ontogeny of higher cirripeds (Lepadomorpha and Verrucomorpha; Darwin, 1851).

While *Praeilepas* of the Carboniferous retained chitinous valves throughout life, and the peduncle was unarmored (Schram, 1975), in extant 5-plated lepadiform barnacles (*Oxynaspis*, *Lepas*, *Poecilasma*, etc.), these same plates are calcified. Darwin (1851) noted that *Oxynaspis*, with its tendency to form subcentral scutal and carinal



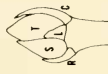





POLLICIPOID SCALPELLIDAE, IN PART							
	ASCOTHORACICA	CYPRILEPADIDAE	LEPADIDAE, OXYNASPIDIDAE, PRAELEPADIDAE, etc.	NO SUBFAMILY	LITHOTRYINAE	CALANTICINAE	POLLICIPINAE
EXTANT GENERA	<i>Synagoga</i> etc. 	NONE	<i>Oxyaspis</i> , <i>Lepas</i> etc. 	NONE	<i>Lithotrya</i> <i>Neolepas</i> 	<i>Calantica</i> etc.	<i>Pollicipes</i> etc.
EXTINCT AND/OR FOSSIL FORMS	<i>Ulophysema</i> (?), BY BURROWS IN ECHINOID TESTS	<i>Cyprilepas</i> 	<i>Praelepas</i> 	<i>Eolepas</i> & <i>Archaeolepas</i> 	NONE		
GEOLOGIC AGE KNOWN	CRETACEOUS	U. SILURIAN	CARBONIFEROUS	U. TRIASSIC- L. CRETACEOUS	→	U. JURASSIC	LEOCENE (? U. TRIAS)
INFERRED	> SILURIAN; ? U. CAMBRIAN	→	→	→	JURASSIC	→	CRETACEOUS
ONTOGENY OF CAPITULAR ORGANIZATION IN <i>Pollicipes</i>	CYPRID LARVA (2 PLATES)	ATTACHED CYPRID (STAGE)	PRIMORDIAL VALVE (STAGE (5 PLATES)	CALCIFIED ROSTRUM (ONE PAIR OF LATERAL) ADDED (6 PLATES)	CALCIFIED ROSTRUM (ONE PAIR OF LATERAL) ADDED (8 PLATES)	SUBCARINA 8 ADDITIONAL LATERAL PLATES ADDED (3 OR MORE PLATES)	SUPPLEMENTARY WHORLS ADDED

FIGURE 5. The ontogeny of *Pollicipes polymorphus* (Linne'), as described by Broch (1922), compared to extant and extinct cirriped taxa. Capitular ontogeny has a part for part correspondence with the phylogenetic sequence. From the phylogeny, a Jurassic age for the Lithotryinae can be inferred.

umbones, was intermediate between lepadiforms and scalpelliforms. It is noteworthy that in *Praeolepas* the carinal umbo is already apical in position, as it is in all generalized scalpellids.

The next, or "*Eolepas* stage" in the ontogeny of *Pollicipes*, corresponds to the oldest fossil scalpellid, *Eolepas*. In this stage the calcareous rostrum has been added, bringing the number of capitular plates to 6. The lack of a chitinous primordium for the rostrum led Broch (1922) to consider the 5 chitinous valves as the primitive condition, a view subsequently substantiated from the fossil record by *Praeolepas*.

The *Eolepas/Archaeolepas* level of organization, which spanned most of the Mesozoic, included a peduncle armed with calcified denticles. It is from peduncular denticles that the additional capitular valves were phylogenetically derived. The capitular organization of *Eolepas* is passed through in the ontogeny of *Pollicipes*, but the peduncle at this stage is unarmored.

In the next or "*Neolepas* stage" in the ontogeny of *Pollicipes*, a pair of median lateral plates is added. This brings the capitular count to 8. There are no recognized fossil representatives of this 8-plated stage, but the *Neolepas* level of capitular organization fills the gap between the *Eolepas* (6-plated) and the *Calantica* (13-plated) stages in ontogeny.

In the next, or "*Calantica* stage," in the ontogeny of *Pollicipes*, a subcarina and 2 pairs of latera have been added thereby duplicating the level of organization in scalpellids reached in the late Mesozoic, a level that has persisted into the Holocene in members of the Calanticinae (Zevina, 1978; Foster, 1978). Many elaborate variations occurred, but no forms representing them survived much beyond the Jurassic or Cretaceous (Newman et al., 1969; Hatton, 1977).

The addition of one or more whorls of numerous small plates around the base of the capitulum completes the ontogeny of *Pollicipes*. This level of organization is known from the fossil record with certainty from the lower Eocene, but it is likely to have been achieved at least by the Cretaceous. Some populations of *Pollicipes* persisted as dominant high intertidal lepadomorphs in the eastern Atlantic, eastern Pacific and Indo-West Pacific today, although Foster (1978) points out that the last species, *P. mitella*, is quite distinct from *Calantica* and *Pollicipes* and should be assigned to the genus *Capitulum* Gray, as proposed by Withers (1928). This is very interesting because *Capitulum* could readily be derived from *Neolepas* by the elevation of a single whorl of peduncular scales to the capitulum.

Comparing the orderly increase in capitular complexity, in the evolution of the lepadomorphs, with the ontogenetic stages in the postlarval development of *Pollicipes*, supports the decision to insert the *Neolepas* level of organization between that of *Eolepas* and *Calantica*. The *Neolepas* stage is also seen following the *Eolepas* stage in the ontogeny of some species of *Calantica* described by Foster (1978).

The purpose of the foregoing exercise has been to interpret the phylogenetic position of the Lithotryinae in the Scalpellidae and thereby to estimate the probable age of the *Neolepas* level of organization, because it may have no counterpart known in the fossil record. Placing *Neolepas* in the open position between the *Eolepas* and *Calantica* levels of organization in the fossil sequence, allows one to infer an age for the Lithotryinae of at least Jurassic. However, there are specimens referred to *Blastolepas orlovi* Drushchits and Zevina, described by the same authors (1969; figs. 2d (128/11 and 4 (128/15)) from an ammonite from the Lower Cretaceous of the northern Caucasus, that appear to be a lithotryine since they are figured as lacking the carinal latus and subcarina of stramentines such as *Blastolepas*. Drushchits and Zevina infer that these specimens are ontogenetic stages of *Blastolepas*, but the peduncular scales are already formed. Therefore it is very unlikely that they are an ontogenetic stage because addition of plates to the capitulum after the peduncular scales have appeared, is unknown in extant scalpelliforms. If, upon reexamination of this material, it turns out that the carinal latus and subcarina are actually lacking, the existence of the Lithotryinae in the Lower Cretaceous would appear to have been established. The new

form would be neither *Lithotrya* nor *Neolepas* because the peduncular whorls are each composed of but 8 plates, as in the archaeolepadidine *Archaeolepas* and the stramentines *Stramentum*, *Loricula*, *Squama* and *Blastolepas*.

Specter of Progenesis

A well-preserved ontogenetic sequence has its pitfalls in drawing inferences concerning progressive evolution because there is the possibility of regressive evolution in the form of paedomorphosis (progenesis; Gould, 1977). In the present case, *Pollicipes* could conceivably retrogress to the *Eolepas* level of capitular organization, because it is at this stage in its ontogeny that cirral feeding begins. This is more than far enough back for present purposes because it is a stage below the level of *Neolepas*. Thus, the *Neolepas* level of organization could be achieved through progenesis. Was it?

The capitular and peduncular armament of *Neolepas* is fully developed. All capitular plates are fully approximate and as heavy in construction as in any shallow water or intertidal scalpellid, and much more so than in any abyssal scalpellid. The carina guards the entire dorsal region, from the base to the occludent portion of the tergal margin, and the rostrum does likewise up to the occludent portion of the scutal margin. The large latera fully guard the basal junction between the scuta and terga, where the capitulum joins the peduncle. Peduncular scales fit as closely as possible around the base of the capitulum, in the peduncular growth region, and as successive whorls enlarge as the capitulum moves upwards, they immediately take on a strongly spined imbricating form. All available plates are arranged to optimize fully their protective capabilities and there are no indications that any have been lost in the optimization process. There is no evidence then to suggest that *Neolepas* is progenetic.

This is in contrast to the situation in *Lithotrya* whose identical capitular organization shows retrogression in the rudimentary nature of the rostrum and latera. The cause of the retrogression is its adaptations to burrowing. However, retrogression in some plates leads to the distinct possibility of loss of others in this genus, and a study of its ontogenetic stages might shed some light on the matter. But there is presently no evidence that *Lithotrya* has lost any capitular plates, as far as adult morphology is concerned, and I can only conclude that *Lithotrya* has descended from a pre-*Calantica*, *Neolepas*-like form.

The dwarf, parasitic males of *Calantica* are another matter (see descriptions by Foster, 1978) because many progress no further than the *Eolepas* or *Neolepas* ontogenetic stage. But their capitular plates are barely approximate and their peduncles are scaleless, all of which suggests that progenesis is responsible for their reduced form.

In the final analysis, there is no way of proving whether or not Lithotryinae consists of progenetic forms. Even the discovery of a fossil of a *Neolepas*-like species of the appropriate geologic age would not be proof of the matter. But all the evidence we do have strongly favors the conclusion that *Lithotrya* and *Neolepas* are relics of a late Mesozoic radiation.

EGG SIZE, SEASONALITY AND RECRUITMENT

Barnes and Barnes (1968) have noted that the number of eggs produced by barnacles is in good part a function of individual size, that frequency of brood production is apparently greatest under optimal conditions and that size of eggs appears to decrease with decreasing latitude. These generalities are based mainly on high and mid-latitude species having planktotrophic nauplius larvae. They have been correlated primarily with the parceling of adult metabolic resources to larvae and the productivity of the waters into which they will be released, particularly along latitudinal gradients. No consideration has been made of the broader issues of biogeography concerned with differences in dispersal requirements for continental, insular and pelagic species. Furthermore, no attention has been paid to deep-sea barnacle species, other than to note

that deep-sea barnacles generally hatch as cyprids (Hoek, 1883; Newman and Ross, 1971). Any correlation between what has been observed in *Neolepas* with what is known in cirripeds in general will be tenuous at best because all we have to work with is the number and size of eggs from a single brood taken from the largest specimen and the range in size of juveniles in the single sample.

In a recent paper, Achituv and Barnes (1978) tout the eggs of a western Indian Ocean intertidal species, *Tetraclita rufotincta* (Pilsbry), as being exceptionally large. They are nearly 19× the volume of those of other species of *Tetraclita* (a subtropical/tropical genus), and >3.5× that of relatively high latitude forms such as *Balanus balanus* (Linné) and *Semibalanus balanoides* (Linné). The eggs of *T. rufotincta* are ellipsoids, as cirriped eggs usually are. They measure about 464 by 316 μm when first laid and 477 by 362 μm when eyed or approaching hatching. It appears that the nauplii of *T. rufotincta* are planktotrophic (Y. Achituv, *personal communication*).

The newly laid eggs of *Neolepas* measured approximately 500 by 300 μm. Therefore *Neolepas* is comparable to *T. rufotincta* in having exceptionally large eggs. Number of eggs per brood is not comparable, however, and we know neither the form nor the trophic capabilities of the larva that hatches. Achituv and Barnes (1978) report the number of eggs per brood in *T. rufotincta* over a wide range of sizes. The count increases from approximately 1000 per brood in the smallest individuals to nearly an order of magnitude more in the largest. The number of eggs in the largest and only specimen of *Neolepas* having them was approximately 440, half that of the smallest *T. rufotincta*. However, *T. rufotincta*, at least on the shores of Elat, has a breeding season of but 2 months a year. It is therefore tempting to suggest that breeding in *Neolepas* is likely seasonless, as has been noted in some other deep-sea invertebrates (Rokop, 1974). By producing numerous broods per year *Neolepas* would be in a position to make up for its relatively small clutch size.

That larval availability is continuous throughout the year is strongly supported by the wide range of sizes (3.5 to 58 mm high) observed in the single sample of 6 specimens of *Neolepas*. Recruitment must be, if not continuous, at least over a long period of time. This is contrary to the conclusion reached by Corliss et al. (1979) who, because of the distinctly different populations of uniformly sized individuals at different vents, suggested that colonization was often effectively a single event. This may be the case for some of the community dominants, but it does not appear to be so for *Neolepas*.

It is important to note that *T. rufotincta*, in addition to producing large eggs, is also unusual for a *Tetraclita* in being distributed on numerous islands of the western Indian Ocean as well as continental shores. Large eggs in this case, and consequently large larvae, may be an adaptation to long-range dispersal, rather than simply to relatively sterile tropical waters as suggested by Achituv and Barnes (1978). If so, this may be in good part the explanation for the exceptionally large egg size in *Neolepas* whose "islands" are apparently hydrothermal springs.

NEOLEPAS AND THE HYDROTHERMAL ENVIRONMENT

Immigration into Hydrothermal Environments

An interesting question concerns how species or their ancestors first became adapted to the hydrothermal regime. It seems there are but 2 possibilities: (1) they either entered from shallow water in situations such as where islands are forming along ridge crests and rift zones intersect continental crust. Under such conditions they could first become adapted to the hydrothermal environment and then to the deep sea, or (2) they have been derived from deep-sea forms that became further adapted to the hydrothermal regime. The first option is the most parsimonious because there is a greater diversity of relatively eurytopic forms in shallow water to choose from and, in terms of gradients, the transition is less severe. But the deep-sea route is open and it is unlikely that nothing has taken advantage of it.

The new barnacle, *Neolepas*, is a scalpellid and the pollicipoid section of the family (Lithotryinae, Calanticinae and Pollicipinae; Zevina, 1978) is represented by 9

extant genera. Although 5 of these are exclusively intertidal or shallow water, 3 have wide bathymetric ranges, from less than 500 metres into abyssal depths (Zevina, 1978a). However, the latter are at a higher level of organization than the Lithotryinae. Therefore, because *Lithotrya* is intertidal and was likely derived from a shallow-water form comparable to *Neolepas*, it seems most probably that *Neolepas* was derived from a shallow-water lithotryine radiation of which *Lithotrya* is the sole surviving shallow-water representative.

Lithotrya, in inhabiting intertidal limestone in the western Atlantic and Indo-West Pacific, and in having no surviving shallow-water relatives, is apparently a relic that has escaped predation pressures of the reef environment by burrowing (Newman, 1960). This view, that *Lithotrya* is a relic, is shared with Foster (1978:122) who wrote: "The tropical rock-boring genus *Lithotrya* may . . . be an intertidal refugee of early scalpellid evolution, finding protection by boring into coral boulders. The few capitular plates . . . in addition to the basic five, may be a pre-pollicipoid condition in scalpellid evolution." Interestingly, appropriate predation pressures are inferred to have dramatically increased in the late Mesozoic (Vermeij, 1977), a time when the lithotryines are inferred to have evolved from the now wholly extinct *Eolepas* level or organization. It seems likely that it was during this late Mesozoic revolution that *Lithotrya* found its refugium in burrowing and *Neolepas* found refuge near hydrothermal springs in relatively shallow water.

Neolepas and some Metals of the Hydrothermal Environment

Rock-5, the substratum from which the sample of specimens of *Neolepas* was taken, was not clearly associated with an active hydrothermal vent. Unfortunately, there are no temperature data for this particular site, but the temperature field was estimated to range from near ambient (1.5°C) to as high as 5°C (R. Ballard, *personal communication*). The rock itself consisted of a clump of thickly encrusted empty worm tubes. The crust, at least that to which the largest barnacles were attached, proved to be a ferriferous deposit having a metallic composition of Fe, Si, Ca, Mn and Mg, in order of decreasing abundance. Aluminum was nearly equal in relative concentration to Mg, but Na, P, K, Cu and Zn were in trace amounts (Analytical Facility, SIO: Cambridge [S-4] SEM and Ortec Energy Dispersive X-ray Analyzer). The deposition of largely Fe rather than other metals such as Zn and Cu would be expected at the cooler end of the hydrothermal spectrum (R. Ballard, *personal communication*).

A similar appearing deposit was already noted as occurring on the shell of the barnacles, there being more on the older than the younger parts. The peduncular scales are particularly appropriate in this regard because they are graded in age. A series of scales was therefore sampled for SEM/X-ray analysis. A single scale was taken at intervals of 1 cm along the holotype specimen, beginning in the growth zone just below the capitulum and ending near the point of attachment to the substratum. The first scale, from the growth zone and therefore the youngest in the series, had a composition of Ca, S and Si, P and Fe, 5 of the 8 elements analyzed for. Iron moved up in relative concentration over the next 3 (older) intervals. Interestingly Mn appeared and then increased along with Fe so that the metallic composition of the crust on the older scales was commonly Fe, Mn, Ca, Si and Mg; a ferromanganese deposit. As noted above and by Francheteau et al. (1979), Mn is in relatively low abundances at 21°N. The high concentrations that develop on the scales of *Neolepas* are therefore curious. They may be due to bacterial activity because the scales of *Neolepas* are calcite (J. Hawkins, *personal communication*) and it has recently been demonstrated that calcite is required for Mn oxidation by pure cultures of marine bacteria (Nealson and Ford, *in press*).

The barnacles were being incrustated with ferromanganese deposits rather than salts or oxides rich in Zn and Cu reported from the high end of the hydrothermal temperature spectrum. Therefore the chemistry of the animals themselves was examined. Three samples were taken from the holotype of *Neolepas*—the left scutum (not destroyed in

the process), the scutal adductor muscle and a slice of the prosomal region including a portion of the digestive gland. These same structures were also sampled from *Pollicipes polymerus*, a local intertidal relative of *Neolepas*. While scanning for metals, the proportions of Mg, and S to Ca were determined. The two species were quite similar except that Mg was higher in *Neolepas* than in *Pollicipes*, but Mg was higher than S only in the digestive gland and adductor muscle of *Neolepas*. Zinc was detected only in the digestive gland of *Neolepas*. Thus it appears that while *Neolepas* is ingesting and assimilating some Mg from the hydrothermal environment, it is ingesting but not assimilating Zn because there were no significant amounts in the musculature and exoskeleton.

The source of the Zn found in the digestive gland must be from ingested material from the surrounding water, presumably inorganic particles and the food, because there are only traces in the immediate substratum. The food is probably in good part bacteria that may be clinging to and extracting free energy from suspended zinc sulfide and similar oxidizable particles (K. H. Neilson, *personal communication*). Bacteria utilizing H₂S may also be involved (Corliss et al., 1979). It is notable that the filter feeding appendages and mouthparts of *Neolepas* are especially adapted to handle extremely fine particles.

ACKNOWLEDGMENTS

Thanks are due to Drs. F. Grassle and R. Hessler for allowing me to work on this material. I am most grateful to Dr. R. Ballard for collecting the specimens of *Neolepas*; to Drs. J. Hawkins, P. Lonsdale and K. Neilson for discussions about hydrothermal environments; to R. La Borde (Analytical Facility, SIO) for advice on the chemical analyses; to Drs. F. Schram and R. Hessler for helpful criticisms of the first draft of the manuscript; and to Drs. R. Scheltema and R. Strathmann for general discussions on reproductive strategies in marine invertebrates. The photo (Fig. 1) of *Neolepas* was taken by Mr. Larry Ford (Photographic Laboratory, SIO), and the drawings were prepared by Ms. Nancy Freres. Thanks are also due the Rise Project Group, supported by National Science Foundation grants OCE 78-01664, 78-21082 and 79-00984, for bringing together the technology and expertise that made the collection of the specimens of *Neolepas* possible. Support from the National Science Foundation (DEB 78-15052) for work on the systematics of cirripeds is gratefully acknowledged.

LITERATURE CITED

- Achituv, Y., and H. Barnes, 1978. Some observations in *Tetraclita aquamosa rufotincta* Pilsbry. *Journal of Experimental Marine Biology and Ecology* 31:315-324.
- Barnes, H., and M. Barnes, 1968. Egg numbers, metabolic efficiency of egg production and fecundity: Local and regional variations in a number of common cirripedes. *Journal of Experimental Marine Biology and Ecology* 2:135-153.
- Broch, Hj., 1922. Studies on Pacific cirripeds, papers from Dr. Th. Mortensen's Pacific Expedition 1914-1916, No. X. *Dansk naturhistorisk forening. Videnskabelige meddelelser* 73:215-358.
- Corliss, J. B., J. Dymond, L. I. Grodon, J. M. Edmond, R. P. vonHerzen, R. D. Ballard, K. Green, D. Williams, A. Bainbridge, K. Crand, and T. H. vanAndel, 1979. Submarine thermal springs on the Galápagos Rift. *Science* 203:1074-1083.
- Darwin, C., 1851. A Monograph of the Subclass Cirripedia, with figures of all species. The Lepididae; or, pedunculated cirripeds. Ray Society, London, v-xi, 1-400 pp., 1-X pls.
- Drushchits, V. V., and G. B. Zevina, 1969. New Lower Cretaceous Cirripeds from the Northern Caucasus. *Paleontological Journal* (2):73-85 (Moscow).
- Ekman, S., 1953. *Zoogeography of the Sea*. Sidgwick and Jackson, Ltd., London, 417 pp.
- Foster, B. A., 1978. The Marine Fauna of New Zealand: Barnacles (Cirripedia: Thoracica). Memoir 69. New Zealand Oceanographic Institute, Wellington, 160 pp.
- Francheteau, J., H. D. Needham, P. Choukroune, T. Juteau, M. Séguret, R. D. Ballard, P. J. Fox, W. Normark, A. Carranza, D. Cordoba, J. Guerrero, C. Rangin, H. Bougault, P. Cambron, and R. Hekinian, 1979. Massive deep-sea sulphide ore deposits discovered on the East Pacific Rise. *Nature* 277:523-528.
- Gould, S. J., 1977. *Ontogeny and Phylogeny*. Harvard University Press, Cambridge, Massachusetts, 501 pp.
- Gravel, A., 1905. *Monographie des Cirripèdes ou Thecostracés*. Masson et Cie., Paris, xii, 472 pp. 427 figs.
- Hattin, D. C., 1977. Articulated lepadomorph cirripeds from the Upper Cretaceous of Kansas:

- Family Stramentidae. *Journal of Paleontology* 51:797-825.
- Hoek, P. P. C., 1883. Report on the cirripeds collected by H.M.S. Challenger during the years 1873-1876. Report on the Scientific Results of the Voyage of H.M.S. Challenger, *Zoology* 8. 169 pp.
- Madsen, F. J., and T. Wolff, 1965. Evidence of the occurrence of Ascothoracica (parasitic cirripeds) in the Upper Cretaceous. *Saertryk af Meddelelser fra Dansk Geologisk Forening* 15:557-558.
- McLaughlin, P., and D. Henry, 1972. Comparative morphology of complementary males in four species of *Balanus* (Cirripedia Thoracica). *Crustaceana* 22:13-30.
- Nealson, K. H., and J. Ford. Surface enhancement of bacterial manganese oxidation: Implications for aquatic environments. *Geomicrobiology (in press)*.
- Newman, W. A., 1960. The paucity of intertidal barnacles in the tropical Western Pacific. *Veliger* 2:89-94.
- Newman, W. A., 1974. Two new deep-sea Cirripedia (Ascothoracica and Acrothoracica) from the Atlantic. *Journal of the Marine Biology Association of the United Kingdom* 54:437-456.
- Newman, W. A., and A. Ross, 1971. Antarctic Cirripedia. Antarctic Research Series 14. American Geophysical Union. 257 pp.
- Newman, W. A., V. A. Zullo, and H. H. Withers, 1969. Cirripedia, in *Treatise on Invertebrate Paleontology* (R. C. Moore, ed.), Part R. Arthropoda 4:R206-R295. Geological Society of America.
- Normark, W. R., 1976. Delineation of the main extrusion zone of the East Pacific Rise at lat. 21°N. *Geology* 4:681-685.
- Pilsbry, H. A., 1907. The barnacles (Cirripedia) contained in the collections of the United States National Museum. *Bulletin United States National Museum* 60:122 pp., pls. 1-11.
- Pilsbry, H. A., 1908. On the Classification of Scalpelliform Barnacles. *Proceedings of the Academy of Natural Sciences* 60:104-111.
- Rokop, F. J., 1974. Reproductive patterns in the deep-sea benthos. *Science* 186:743-745.
- Schram, F. R., 1975. A Pennsylvanian lepadomorph barnacle from the Mazon Creek Area, Illinois. *Journal of Paleontology* 49:928-930.
- Sylvester-Bradley, P. C., 1961. Archaeocopida, in *Treatise on Invertebrate Paleontology* (R. C. Moore, ed.), Part Q. Arthropoda 3:Q100-Q103. Geological Society of America.
- Vermeij, G. J., 1977. The Mesozoic marine revolution; evidence from snails, predators and grazers. *Paleobiology* 3:245-258.
- Wills, L. J., 1963. *Cyrrilepas holmi*, Wills, 1962, a pedunculate cirripede from the Upper Silurian of Oesel, Estonia. *Palaeontology* 6:161-165.
- Withers, T. H., 1928. *Catalogue of Fossil Cirripedia in the Department of Geology, 1. Triassic and Jurassic*. 154 pp. + 12 pls. British Museum (Natural History), London.
- Zevina, G. B., 1978a. 1. A new classification of the Scalpellidae (Cirripedia, Thoracica). Subfamilies Lithotryinae, Calanticinae, Pollicipinae, Scalpellinae, Brochiinae and Scalpellinae. *Zoologicheskyy Zhurnal Akademii Nauk SSSR* 57(7):998-1007 (in Russian with English abstract).
- Zevina, G. B., 1978b. A new classification of the Scalpellidae (Cirripedia, Thoracica). 2. Subfamilies Arcoscalpellinae and Meroscalpellinae. *Zoologicheskyy Zhurnal Akademii Nauk SSSR* 57(9):1343-1352 (in Russian with English abstract).

Scripps Institution of Oceanography A-002, La Jolla, California 92093 USA, and Natural History Museum, Box 1390, San Diego, California 92112.

ADDENDUM:

Three interesting pieces of lore bearing on cirriped evolution came to my attention after this article went to press. The first, thanks to Dr. F. Schram (San Diego Natural History Museum), is a paper by M. A. Whyte (1976, A Carboniferous pedunculate barnacle. *Proceedings of the Yorkshire Geological Society* 41, part 1. (1):1-12 + pls. 1 & 2), describing what appears to be the first Paleozoic scalpelliform lepadomorph. Whyte interprets it to be at the *Eolepas/Archaeolepas* level of scalpellid organization, including peduncular scales as well as a capitulum of 6 plates (the basic 5 plus the rostrum; Table 1 herein). This places the origin of the scalpelliforms some 50 million years earlier than previously recognized and then virtually contemporaneous with the more primitive lepadiform *Praelepas* (5 capitular plates and naked peduncle). However, with the more generalized Cyrrilepadidae (one pair of capitular plates and naked peduncle) appearing in the Silurian, there is at least a 100-million-year span in which the lepadiforms can make their appearance before the scalpelliforms, as indeed they must have.

Actually there appears to have been even more time available than this (Silurian to Carboniferous) for the lepadiforms to appear, since the second piece of lore concerns an apparent pedunculate barnacle from the Burgess Shale being described by Desmond Collins and David Rudkin (Royal Ontario Museum). Dr. Collins, at the suggestion of Dr. A. J. Southward (Plymouth), kindly allowed me to see pictures of what I cannot fault as a pedunculate barnacle. Thus the origin of the cirripeds must have been in the earliest Paleozoic as inferred herein (Table 1).

The third piece of lore further heightens appreciation of the ancient roots of the cirripeds. Mr. Mark Grygier (Scripps Institution of Oceanography) has discovered that an ascothoracican, *Dendrogaster* sp. from the Ross Sea, has a generalized flagellated spermatozoan otherwise unknown to the Crustacea, and he has since received a personal communication from Dr. K. G. Wingstrand (Copenhagen) that another ascothoracican, *Ulophysena* from the North Atlantic, likewise has flagellated sperm. Thus the cirripeds are not only very old but they must have stemmed from a reproductively unspecialized stock.